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Tree radial growth is projected to decline in South Asian moist forest trees under climate change

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ABSTRACT

Global climate change has been reported to affect tree growth around the world and such impacts are predicted to be intensified under future climate change particularly in the tropics. It is therefore important to study the climate-growth relationships of tropical trees to understand how they have responded to the past climate variability and to predict how they will respond to future climatic changes. We investigated tree radial growth responses to regional climatic changes in Bangladeshi moist tropical forests. We selected three species based on their distinct growth-ring boundaries and their wide distribution around the tropics. First, we simulated growth responses to climate for the past 66 years (1950–2015) based on the climate-growth relationships. Next, we projected tree-growth until the end of current century (2016–2100) under different climate change scenarios (Representative Concentration Pathways, RCP). All the three species produced statistically robust ring-width index chronologies covering the current and the past century. Climate-growth analysis revealed that temperature (monthly, annual and seasonal) significantly negatively affected tree radial growth in all three species. Precipitation prior to the current growing season negatively and current year post monsoon precipitation positively influenced radial growth. Tree radial growth was also influenced by Niño 3.4 region Sea Surface Temperature (SST) anomalies mainly through the modulation of local climate. We projected tree radial growth to be declined in all three species by 20% under high concentration scenario (RCP 8.5) followed by 11.3% and 9% under medium (RCP 6.0) and low-medium concentration scenarios (RCP 4.5). If these species show similar growth responses to climatic changes in other native ranges across the tropics, this could have severe consequences for the carbon balance of tropical forests.

1. Introduction

Understanding tropical forests' response to global change is important since tropical forests are a crucial component of the global carbon cycle, containing about one fourth of the global terrestrial carbon (Pan et al., 2011; Brown and Lugo, 2017). In the past century, the earth experienced various environmental changes. Since the late 1800's, the mean land surface temperature has increased by 0.85 °C and this warming trend is predicted to be continued throughout the current century (IPCC, 2013). Tropical forests are currently under stress due to experiencing most rapid warming rates in recent geological times (Marcott et al., 2013) and possibly face unprecedented warming in the near future (Diffenbaugh and Scherer, 2011). Current knowledge of plant functioning suggest that continued warming will alter the net carbon balance (Grace et al., 2014; Wood et al., 2012) and reduce the net primary productivity of tropical forests (Doughty et al., 2015).

Tropical moist forests became one of the warmest terrestrial ecosystems and might already have negatively responded to global warming (Corlett, 2011; Saxe et al., 2001). Warming may reduce assimilation rates (Galbraith et al., 2010; Doughty, 2011), increase autotrophic respiration rates (Lloyd and Farquhar, 2008) and evaporative demand (Galbraith et al., 2010; Choat et al., 2012), leading to tree growth decline. Some recent studies reported carbon storage reduction due to decline in tree growth in tropical forests across the continents (Brienen et al., 2015; Baccini et al., 2017). Because these forests account for one third of the global terrestrial net primary productivity (Bonan, 2008), any of such responses could strongly affect atmospheric CO_2 levels and future climate. In view of evidence that tropical forests may already be near a high temperature threshold, this biome might be more vulnerable to climate change than previously expected (Clark et al., 2003; Doughty and Goulden, 2009).

It has already been documented that temperature increase caused

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growth decline in some tropical forests of Central Amazonia, South America and South Asia (Chambers and Silver, 2004; Clark et al., 2003, 2010, 2013; Feeley et al., 2007; Dong et al., 2012; Rahman et al., 2017). Besides, severe drought conditions related to extreme El Niño events reduced tree growth throughout the tropics (Phillips et al., 2009; Vincent et al., 2009; Brienen et al., 2010; Pucha-Cofrep et al., 2015; Mokria et al., 2017). However, also increasing wood productivity was reported in some plot based and experimental studies (Körner, 2006; Huang et al., 2007; Phillips et al., 2008; Lewis et al., 2009). These contrasting results clearly demonstrate the need of further studies to better understand site- and species-specific responses of tropical forests to future climate change. Currently, our ability to predict growth response of tropical forest trees to rising temperatures and other environmental changes is limited, due to lack of long-term growth data in many tropical forests (Saxe et al., 2001). In the absence of in-situ tree-level warming experiments and limited availability of long-term permanent sample plots, dendrochronology offers the opportunity to obtain individual tree-growth data for longer time scales and in annual resolution in many tropical environments.

Dendrochronology in the tropics is a growing field of science and has already been successfully applied in South and Southeast Asia, tropical South America, and subtropical to semi-arid Africa (Worbes, 2002; Boninsegna et al., 2009; Rozendaal and Zuidema, 2011; Pumijumnong, 2013; Gebrekirstos et al., 2014; Brienen et al., 2016; Fichtler, 2017). In a dendrochronological context, moist tropical forests are less studied to date than dry tropical forests. Although annual growth-ring formation has been confirmed for an increasing number of moist forest species (Zuidema et al., 2012; Brienen et al., 2016; Islam et al., 2018), studies on their response to climatic and environmental changes are still limited to rather few species (Brienen et al., 2016). Hence, our current understanding of how moist forest trees will respond to future climatic changes is still very limited.

One prerequisite for projecting future responses of tropical moist forest trees is the understanding of how they responded to the substantial inter-annual climatic variations in recent decades. Without studying the climate–growth relations, no inferences can be made on the likely impact of future climatic changes on tropical moist forest trees. Given the huge biodiversity of tropical forests, climate-tree growth analysis need to be extended to more species and regions highly vulnerable to climate change. Here we present a dendroclimatological study conducted in the moist tropical forests in Bangladesh that are influenced by the Asian monsoon climate. We combined dendrochronological and modelling approaches to understand the relations between tree-growth and inter-annual climate variability and to predict future tree-growth under climate change scenarios. We tested three hypotheses: (1) the radial growth series of individuals of selected tree species synchronize and subsequent Ring-width Index (RWI) chronologies contain common environmental signals, (2) tree radial growth is sensitive to local and global climate variables (3) radial growth of the selected trees species will decline in future under high and moderate climate change scenarios.

2. Materials and methods

2.1. Study area and climate

The study was conducted in Rema, Chonbari and Kalenga forest reserves, 1795 ha of which are declared as nature reserve named the Rema-Kalenga Wildlife Sanctuary (RKWS) (Fig. 1). The area is located between 24°06′-24°14′ N and 91°36′-91°39′ E in the Sylhet Hills, a bio-ecological zone of Northeastern Bangladesh (Nishat et al., 2002) and part of the Indo-Burma biodiversity hotspot. The study area consists of hills below 100 m a.s.l. elevation as well as the flood plain valleys. Soils on the hills are sandy loamy, whereas those on the low lying area are clay loamy (Hassan, 1994). Following the life zone classification of Holdridge (Holdridge, 1967), the forests can be classified as moist tropical forests. The forests are mixed deciduous where the forest canopy is mainly comprised of deciduous trees (canopy height varied between 40 and 50 m) and evergreen trees and shrubs form the forest understory. The top canopy is composed of *Dipterocarpus turbinatus* C.F.Gaertn., *Schima wallichii* (DC.) Korth., *Tectona grandis* L.f., *Chukrasia tabularis* A.Juss., *Toona ciliata* M. Roem., *Hopea scaphula* Roxb., *Albizia procera* (Roxb.) Benth., *Syzygium grandis* (Wight) Walp., *and Gmelina arborea* Roxb. *Syzygium cumini* (L.) Skeels., *Terminalia bellirica* (Gaertn.) Roxb., *Lagerstroemia speciosa* (L.) Pers., *Lagerstroemia parviflora* Roxb., *Dillenia pentagyna* Roxb., and different *Ficus* species form the middle canopy. The lower canopy is mainly composed of different bamboo species (*Bambusa sp.*).

The annual mean temperature in the study area is 24. 8 °C and annual precipitation amounts 2363 mm. Dry season (monthly precipitation < 100 mm) is shorter (November–March) than the wet season (April–October) (Fig. 2). A significant increasing trend was observed in average annual mean, minimum and maximum temperatures. However, no significant trend was observed in annual precipitation amount (Fig. 2).

2.2. Climate data

Climate data of Sreemangal meteorological station such as precipitation and temperature were collected from the Bangladesh Meteorological Department (BMD). All temperature data (mean, minimum and maximum) were detrended since there was a significant increasing trend over 1950–2015. A cubic smoothing spline function was used for the detrending. Niño 3.4 region sea surface temperature (SST) anomalies were obtained from the Climate Prediction Center (CPC) of the National Oceanic Atmospheric Administration (NOAA). The Asia-Pacific Data-Research Center (APDRC) of the International Pacific Research Center (IPRC) was accessed for the Indian Summer Monsoon Index (ISMI) data. The ISMI data was normalized for the period 1948–2015. We also accessed the Climatic Research Unit (CRU) Time-Series (TS) Version 4.00 (CRU TS4.01) to obtain high resolution gridded temperature and precipitation data and self-calibrating Palmer Drought Severity Index (PDSI) data (van den Schrier et al., 2006). HadCRUH relative humidity anomalies and HadSST.3.1.1.0 sea surface temperatures (SST) anomalies were accessed through KNMI Climate Explorer (The Royal Netherlands Meteorological Institute; http://climexp.knmi.nl/).

2.3. Sample collection and preparation

We collected wood samples of three species, namely *Chukrasia tabularis*, *Toona ciliata*, and *Lagerstroemia speciosa*, selected based on their distinct growth-ring boundaries as identified by a preliminary study of 27 tree species (Islam et al., 2018) and their wide distribution throughout the tropics. *C. tabularis* can tolerate partial shade while *T. ciliata* is a light demanding pioneer tree. Both *C. tabularis* and *T. ciliata* occupy the top canopy of the forest. Unlikely, *L. speciosa* is a shade tolerant species which occupies both the top and the middle canopy depending on the site. Growth-ring boundaries were mainly delineated by marginal parenchyma in *C. tabularis* and by larger early wood vessels in *T. ciliata* and L. *speciosa* (Islam et al., 2018) (Fig. 3). Annual growth-ring formation was confirmed in all species (Baker et al., 2005; Bhattacharyya and Yadav, 1989; Heinrich and Banks, 2006; Rahman et al., 2017; Shah and Mehrotra, 2017; Vlam et al., 2014). A detailed description of these species is given in Table 1.

A total of 210 increment cores and one stem disc of *C. tabularis* were collected. Cores were extracted from 105 trees approximately at breast height (1.3 m) by using a 5.0 mm diameter Suunto increment borer (Vantaa, Finland). We avoided coring of trees with large buttresses and other irregular growth form which hinder the identification of growth rings and crossdating within and between trees. Avoiding buttressed trees may result in biases associated with tree selection (Brienen et al.,

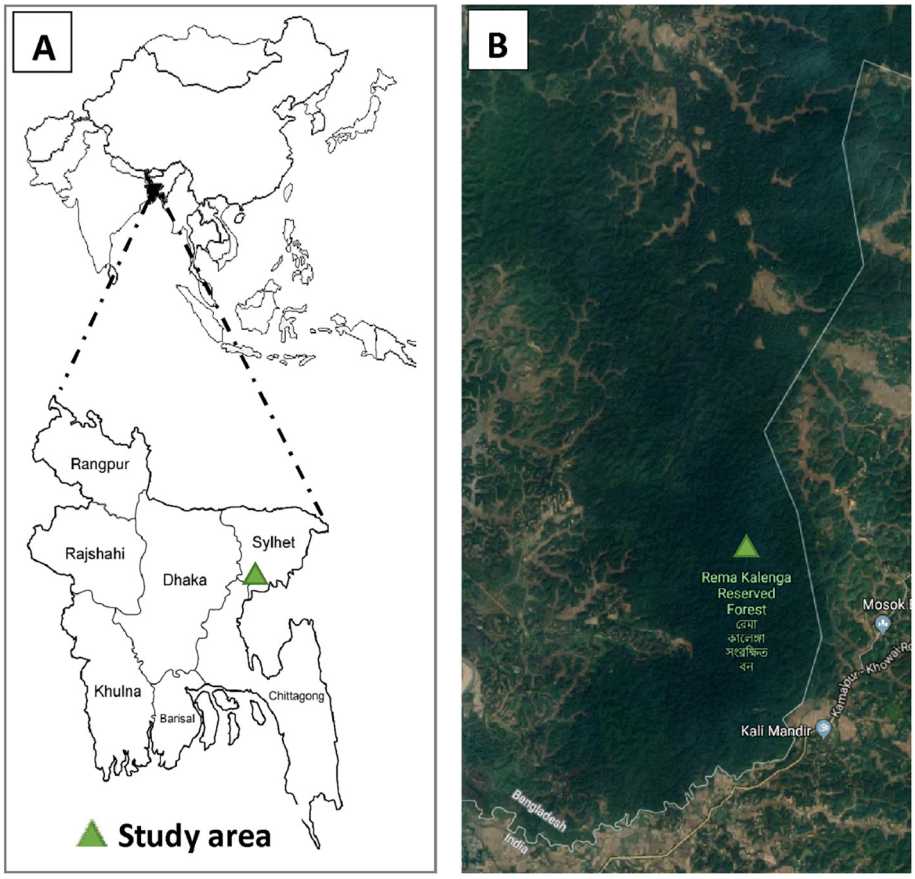

Fig. 1. (A) Map of Asia (upper) and Bangladesh (lower) indicating the location of study area (Rema-Kalenga Wildlife Sanctuary, RKWS). (B) Google earth image showing the forest cover of RKWS.

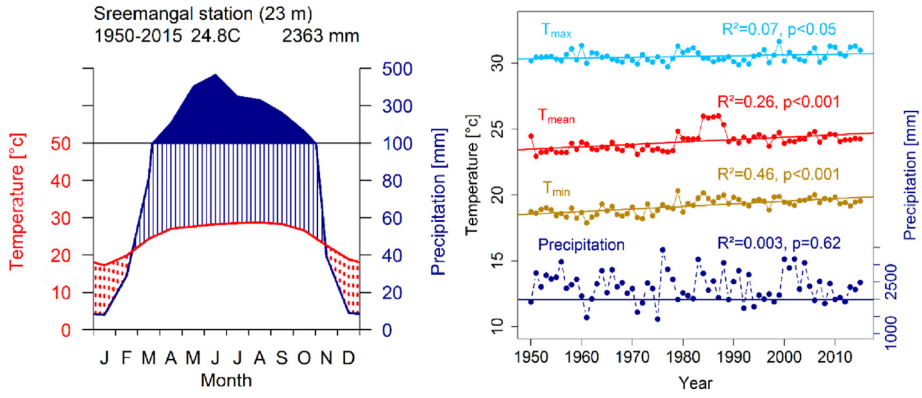

Fig. 2. Climate diagram (left panel) based on data from 1950 to 2015 recorded at the nearest meteorological station (Sreemangal, 23.5 km away from the study site). Right panel shows the trends in climate variables over a period from 1950 to 2015.

2012), because buttressed trees are usually larger and/or older than the trees without buttress (Mehedi et al., 2012). Avoiding such trees may thus limit the length of our final tree-ring series. However, considering the main objectives of our research and the availability of adequate samples, this selection criterion is less likely to affect the results of our study. Cores were carefully handled during and after extraction and immediately stored in plastic core holders. Increment cores were air dried for 24 h so that possible attack by stain fungi can be avoided. After mounting the cores on wooden holders we sanded them with increasingly fine grain paper (80–2000 grit) until wood macro features were clearly visible (Stokes and Smiley, 1968). We also applied a high blast air pressure on the wood surface to remove sand dust from the wood vessels. Prepared core surface were then scanned using a flatbed scanner (Epson Expression 10000XL, USA) at a resolution of 1600–2000 dpi.

2.4. Crossdating and chronology development

We measured tree-ring width from the polished wood surface by using a Lintab 6 measuring system (Rinntech, Heidelberg, Germany) and on the scanned images using the image analysis software CooRecorder (Cybis Elektronik & Data AB, Sweden) with a precision of 0.01 mm. Visual crossdating between two or three cores/series within a tree was performed by using TSAP-Win computer program (RINNTECH e. K. Heidelberg, Germany). Crossdating within a tree was also statistically checked following *t*-test and Gleichläufigkeit values (GLK, sign

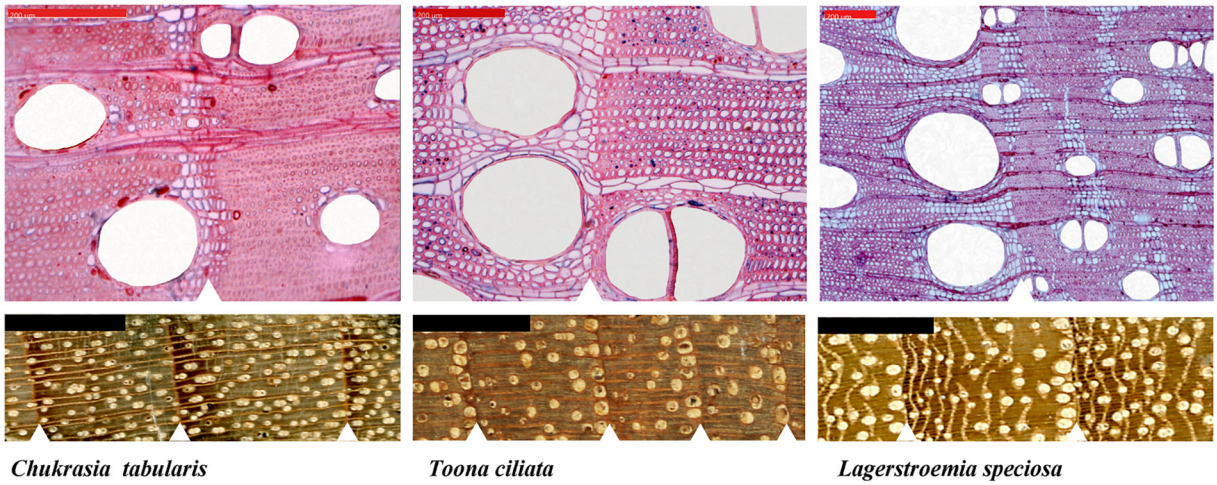

Fig. 3. High resolution digital microscopic images (upper panel) and scanned cross sectional wood surface (lower panel) showing characteristic wood anatomical features of three Bangladeshi moist forest tree species. White triangles indicate growth-ring boundaries. Growth direction from right to left. Scale bars are 200 μm in the microscopic images and 3 mm in the scanned images.

test) (Eckstein and Bauch, 1969) using the same TSAP-Win program. Crossdating cores taken into different direction of the same tree facilitate the detection of false ring structures such as inter annual density fluctuations (Groenendijk et al., 2014) and wedging rings (Worbes, 2002). Concerning the stem disc, we firstly synchronized three ring-width series within the disc and then calculated a mean curve of the disc as a reference to synchronize the ring-width series of the increment cores. Increment cores were crossdated and cores from the same trees were averaged to mean curves. These trees also served as a reference to crossdate subsequent cores of other trees. Only trees with two synchronized and well crossdating cores were considered for further analyses. We used the computer program COFECHA to check the accuracy of crossdating (Holmes, 1983).

Crossdated tree-ring series were detrended to remove biological growth trends from derived tree-ring chronologies by fitting a cubic smoothing spline curve with a 67% frequency response (f = 0.67). The detrending and other statistical test on the raw as well as the detrended time series were performed using the Dendrochronology Program Library in R (dplR) (Bunn, 2008) within the R statistical programming environment (R Development Core Team, 2016). Three ring-width index chronologies, each for one species, were developed with the chron (dplR-package) function using the detrended ring-width index (RWI) series with a robust mean to reduce the influence of outliers (Briffa and Jones, 1990). Spectral analysis was performed to test for any periodicity in the developed chronologies. The expressed population signal (EPS) was calculated which indicates the reliability of a chronology as a fraction of the common variance of a theoretical infinite tree population. The following equation was used to calculate the EPS (Wigley et al., 1984; Briffa and Jones, 1990).

$$EPS = (N \times rbar.\,eff) \div [1 + (N - 1) \times rbar.\,eff]$$

where, N = Number of trees, rbar.eff = effective chronology signal, a signal strength indicator that incorporates both within- and between-tree signals) (Cook et al., 1990).

A running EPS value of 0.85 was used as a threshold (Wigley et al., 1984) to identify the most reliable part of the tree ring chronology (Cook et al., 1990). Mean sensitivity (MS) was calculated to evaluate the year to year variation in radial growth in each chronology (Fritts, 1976). Signal to noise ratio (SNR) was also calculated as measure of the signal strength of the chronology. We examined the influence of the previous year's growth on the current year's growth by calculating first order auto correlation (Fritts, 1976).

2.5. Climate-growth analysis

The relationships between ring-width index chronologies and the monthly and annual climate variables were evaluated by computing simple Pearson's correlation coefficients. A 19 months window (previous year May to current November) was used to correlate radial growth with monthly climate variables. Our study sites receive < 60 mm rainfall during the period from the middle of November to the middle of February (Fig. 2). All three species remain fully or partially leafless during that period. Therefore, we assumed that tree growth temporarily stopped during this period due to cambial dormancy (Worbes, 1999; Volland-Voigt et al., 2011; Trouet et al., 2012). Prior-year climate variables were used in the analysis because tree growth might be influenced by the climate in the preceding growing season (Fritts, 1976). Seasonal correlation analysis was performed by using the "seascorr" function in the "treeclim" package in R (Zang and Biondi,

Table 1
Characteristics of three Bangladeshi moist forest tree species.

Species name	Common name	Family	Distribution[a]	Phenology[b,*]	Ecological guild[c,*]	Max. height (m)	Growth-ring boundary delineating features[d]	Main use of wood[e]
Chukrasia tabularis	Chickrasi	Meliaceae	SA, EA, SEA	Brevi-deciduous	PST	40	MP	F, C
Toona ciliata	Toon	Meliaceae	SA, SEA, Af, A	Deciduous	P	40	P, MP, FWT	F, V
Lagerstroemia speciosa	Jarul	Lythraceae	SA, EA, SEA	Deciduous	ST	26	P, MP, FWT	F, B

[a] SA = South Asia, EA = East Asia, SEA = South-East Asia, A = Australia, Af = Africa, CA = Central America, PN = Papua New Guinea.
[b] Deciduous: tree leafless for more than four weeks; Brevi-deciduous: tree briefly or only partially leafless; Evergreen = trees without leafless periods.
[c] P = Pioneer, PST = Partially shade tolerant, ST = Shade tolerant.
[d] MP = Marginal parenchyma band (terminal or initial), P = Porosity, FWT = Thick-walled latewood fibres.
[e] F = Furniture, C = Construction, V = Veneer & plywood, B = Boat making.
[*] Kalinganire and Pinyopusarerk, 2000; Williams et al., 2008; Orwa et al., 2009).

2015) taking seasonal values integrating 3, 4, 6 months. Following Zang and Biondi (2015), we considered a 14 months window for seasonal analysis starting in October of the previous growth period and ending in November of the current year (termination of the current growing season). The stability of climate-growth relationships was tested by using moving correlation functions following the "treeclim" package in R (Zang and Biondi, 2015). Spatial correlation analysis was performed to evaluate the regional climate signals of the chronologies by using the KNMI climate explorer (Trouet and van Oldenborgh, 2013). All statistical analyses were performed within the R statistical programming environment (R Development Core Team, 2016).

2.6. Growth projections

Based on the climate-growth analysis we developed regression models for predicting tree ring-width indices until the end of current century using different climate change scenarios. Stepwise multiple linear regression was performed on the significant response variables identified in climate-growth analysis. Regression models were trained on an approximately 60% of the data set (1950–1990, calibration period); the resulted models were then tested on the remaining 40% of the data (1991–2015, verification period). After a first calculation, calibration and verification periods were exchanged to cross-validate the reliability and stability of the predicted RWI.

The model performance and skill were tested using multiple statistical tools including Coefficient of determinants (R^2), Significance of models ($p < 0.05$), Reduction of Error (RE), Coefficient of Efficiency (CE), Mean Squared Error (MSE), Product Mean test (PM) and the Durbin-Watson tests (DW). The reduction of error (RE) was used as a measure of the predictive skill of the model (Fritts, 1976; Cook et al., 1990). RE is a verification statistic which measure the relative accuracy of the predictions measured against a reference prediction (Cook et al., 1990). The value of RE can range from negative infinity to a maximum value of 1.0. Negative values of RE indicates the model has little to no skill whereas the positive values suggest the model has predictive skill (Fritts, 1976). We calculated RE using the following equation (Fritts, 1976).

$$RE = 1 - \left[\sum_{i=1}^{n} (x_i - y_i) \div \sum_{i=1}^{n} (x_i - \overline{x_c}) \right]$$

where x_i and y_i are the observed and predicted data in year i of the verification period, and $\overline{x_c}$ is the mean of the observed data in the calibration period.

The CE statistic is similar to RE except that its benchmark for determining model skill is the verification period instead of the calibration period as in RE. The formula for calculating CE can be expressed as follows

$$CE = 1 - \left[\sum_{i=1}^{n} (x_i - y_i) \div \sum_{i=1}^{n} (x_i - \overline{x_v}) \right]$$

where x_i and y_i are the observed and predicted data in year i of the verification period, and $\overline{x_v}$ is the mean of the observed data in the verification period.

The sign test (ST) is traditionally used as a nonparametric test to evaluate the number of agreements and disagreements in sign of departure from the mean in the observed and predicted series (Fritts et al., 1990). We also used the PMT because this robust test accounts for both the signs and the magnitudes of the similarities between the observed and predicted data sets (Fritts, 1976; Cook et al., 1990). MSE is a measure of how close the predicted values are to the observed values; MSE Ratio is the ratio of MSE between verification and calibration period. MSE ratio < 1 indicates the model is valid. The DW test assesses the presence of first order autocorrelation in model's residuals (Durbin and Watson, 1951; Draper and Smith, 1998).

The validated models were then used to simulate growth for the 1950–2015 observed climate period and then projected growth for the period over 2016–2100 under different climate change scenarios. The Coupled Model Intercomparison Project Phase 5 (CMIP5) model outputs of mean temperature and precipitation sum for the closest grid point to our study sites were used (Taylor et al., 2012). We used historical simulations for the period 1950–2015 and future projections for 2016–2100 under three representative concentration pathways (RCPs). Three scenarios include RCP 4.5 (slower emission reductions that stabilize by 2100), RCP 6.0 (slower emission reductions that stabilize by 2100 by higher than in RCP 4.5), and RCP 8.5 (continual increase in emissions to 2100) (Moss et al., 2010; van Vuuren et al., 2011). We used the CMIP5 mean of a set of models used for projecting mean temperatures near earth surface and precipitation sum. RCP 4.5 scenario was developed based on 42 models, RCP 6.0 on 42 models and RCP 8.5 on 39 models. The name of the models and the institutes that provided the model output are listed in Table S1. Outputs of all models are also detailed in http://cmip-pcmdi.llnl.gov/cmip5/index.html.

The number of years with above average growth was calculated for different climate periods (1950–2015, 2016–2060, 2061–2100) and average growth for each climate period was computed. Finally, we calculated growth changes towards the end of current century as follows: $\Delta G = [(G_S - G_P)^* 100]/G_S$

where, ΔG = Percentage growth change, G_S = Simulated growth over 1950–2015, G_P = Projected growth for 2090s.

3. Results

3.1. Characteristics of RWI chronologies

Based on the well synchronized cross-dated tree-ring series of each species (Fig. S1), we developed three species-specific standard ring-width index chronologies (Fig. 4). The statistical characteristics of ring-width series and the statistical parameters used for indicating the signal strength of the chronologies are shown in Table 2 and Table S2. The chronology lengths ranged from 86 to121 years, with *C. tabularis* comprising the longest chronology. All chronologies showed EPS statistics exceeding the widely used threshold value (EPS = 0.85) required to produce a statistically robust RWI chronology (Wigley et al., 1984). The running EPS values of *C. tabularis*, *T. ciliata* and *L. speciosa* dropped below 0.85 before 1923, 1946 and 1926, respectively. Thus, *C. tabularis* had the longest reliable chronology part (93 years) followed by L. *speciosa* (90 years) and *T. ciliata* (70 years).

Mean series inter-correlation (MSI), MS, rbar.eff, SNR and other statistical parameters values were also high (Table 1), indicating the suitability of our chronologies for climate-growth analysis. The independently constructed chronologies were significantly positively correlated among all pairs of species ($P < 0.01$). This similarity in year-to-year growth variations is also reflected by the occurrence of synchronous growth depressions in marker years including 1944–1946, 1984, 1986–1988, and 1999 (Fig. 4).

A 2–4 years periodicity was observed in the wavelet spectra of the RWI chronologies (Fig. 5), corresponding to the ENSO frequency band (D'Arrigo et al., 2005; Maruyama et al., 2011). A higher periodicity of 6–10 years was observed in *C. tabularis* during the period 1910–1935. Because the running EPS falls below 0.85 before 1923, we interpret this result with great caution. We found a decreasing trend in the periodicity in all species. *C. tabularis* and *L. speciosa* contained strong periodicity signals during the period of 1910–1960, whereas in *T. ciliata* the signal remained prominent until the end of past century.

3.2. Tree growth-climate relationships

Tree radial growth was strongly negatively correlated with average annual mean and minimum temperatures in all three studied species (Fig. 6). Average annual maximum temperature significantly affected

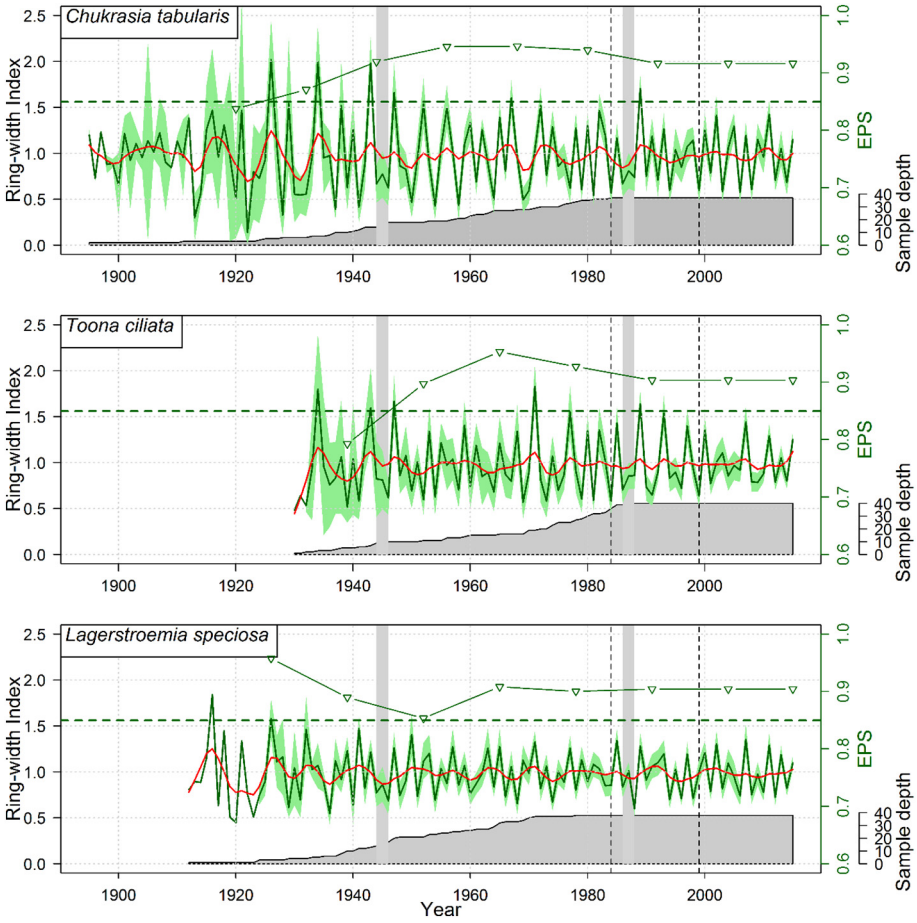

Fig. 4. Standard Ring-width Index (RWI) chronologies of three Bangladeshi moist forest tree species. Light green shaded areas indicate standard deviations of RWI; Red lines represent 7 years smoothing averages; Running EPS are shown above each RWI chronology; Horizontal dashed lines indicate the threshold limit of EPS = 0.85; Vertical dotted lines show growth depressions in marker years (1984, 1999), and vertical shaded areas indicate simultaneous growth suppressions for consecutive years (1944–1946, 1986–1988). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 2
Statistical characteristics of standard ring-width index chronologies of three Bangladeshi moist forest tree species.

Parameters	*C. tabularis*	*T. ciliata*	*L. speciosa*
Time span	1895–2015	1930–2015	1912–2015
Mean length of series (year)	65	50	66
Trees/cores	21/37	26/40	23/38
Mean ring width (mm) ± SD	3.77 ± 1.35	3.98 ± 1.46	2.77 ± 0.76
1st order autocorrelation (AC1)	0.25	0.34	0.47
rbar.bt*	0.33	0.27	0.29
rbar.eff*	0.41	0.35	0.33
Series inter correlation (SIC)	0.54	0.49	0.45
Mean GLK*	0.73	0.65	0.66
Expressed population signal (EPS)	0.91	0.90	0.90
Mean sensitivity (MS)	0.75	0.68	0.53
Signal-to-noise ratio (SNR)	10.43	8.43	8.51

* glk: Gleichläufigkeit (sign test); rbar.bt: mean inter-series correlation between-trees; rbar.eff: effective chronology signal.

radial growth of *T. ciliata* and this species was sensitive to T_{mean}, T_{min}, and T_{max} throughout the growing season (Fig. 6). Current year March temperature was crucial for all species except *L. speciosa* which was more influenced by April T_{mean}. In general, previous year temperatures had only a marginal effect on radial growth. Annual precipitation sum had no influence on the growth of any of the three species (Fig. 5). However, we observed significant negative correlations between current year October precipitation and *C. tabularis* growth. On the other hand, we found positive correlations between previous year July and September precipitation and growth of *T. ciliata*. Likewise, *L. speciosa* growth was positively correlated with previous year October precipitation.

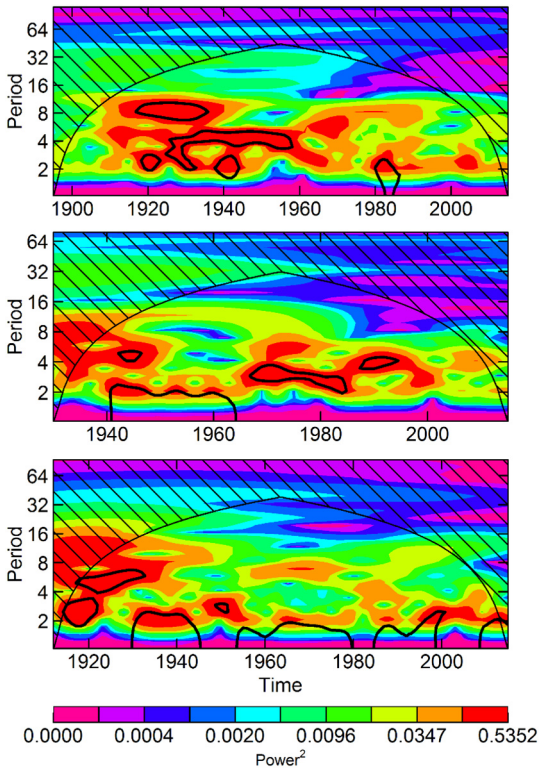

Fig. 5. Wavelet based spectral analysis of standard tree-ring chronologies of three Bangladeshi moist forest tree species. From top to bottom: *C. tabularis*, *T. ciliata*, *L. speciosa*.

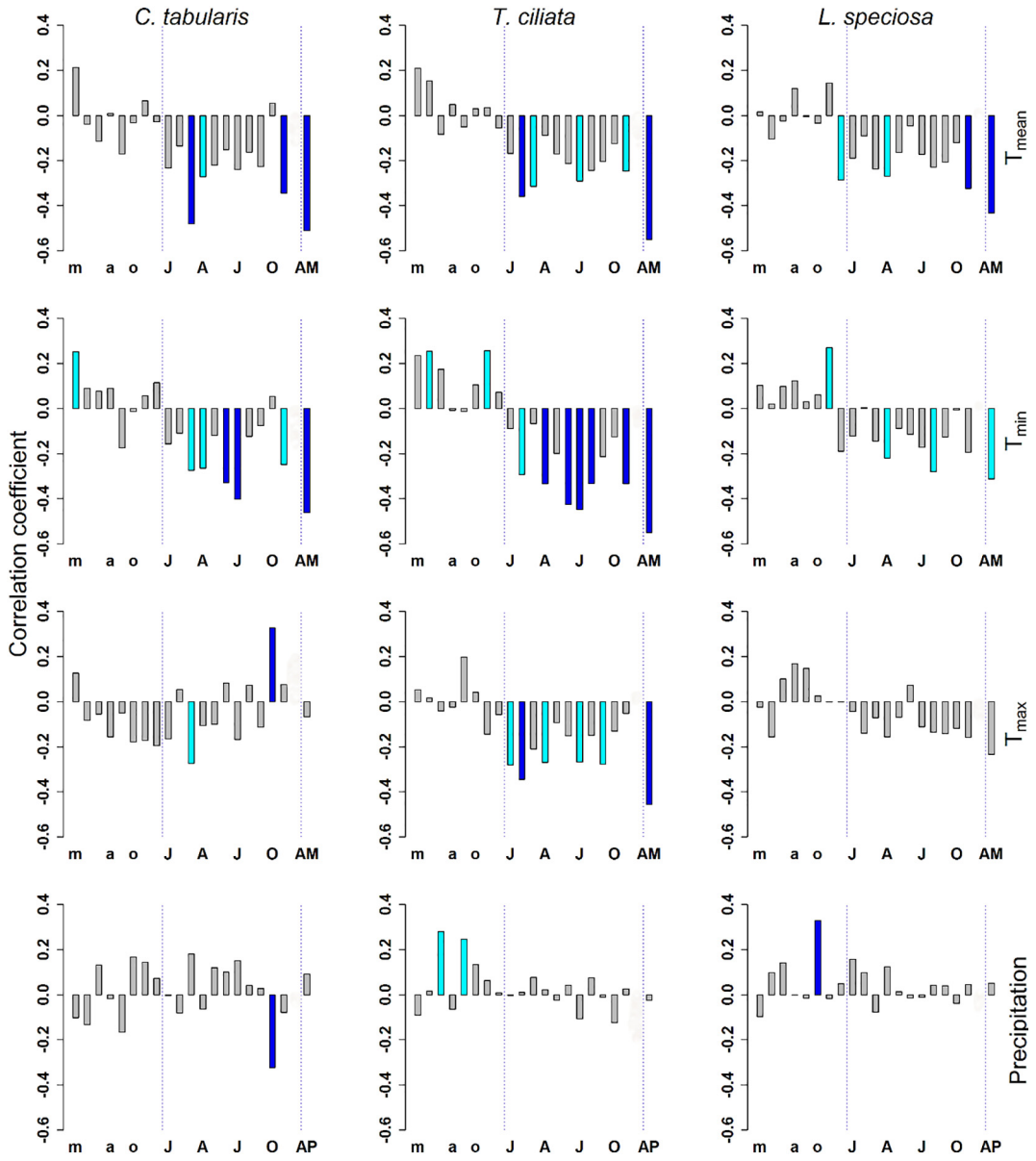

Fig. 6. Correlations between RWI and climate variables. Dark and light blue color bars indicate correlations significant at $p < 0.01$ and $p < 0.05$ level respectively. Lower case letters indicate months of previous year. RWI = Ring-width Index, AM = Annual mean, AP = Total annual precipitation. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Seasonal correlation analysis showed that pre-monsoon and monsoon temperatures had significant negative influences on the growth of all three species (Figs. 5, S2, S3, S4). When averaged over six months, the influence of seasonalized temperatures on tree-growth extended up to the post monsoon season. We observed no significant correlations between seasonalized precipitation and growth of *C. tabularis.* (Fig. S2). However, growth of *T. ciliata* and *L. speciosa* was influenced by previous year post monsoon and dry season precipitation (Figs. S3, S4). Relative humidity and cloud cover were not correlated with tree radial growth in any species we studied. Similarly, we did not observe any significant correlation between PDSI and growth of any species (data not shown).

Spatial correlation analysis with global climate data sets resulted in significant negative correlations between RWI and gridded land surface temperature as in the climate-growth analysis with local instrumental climate data. Both *C. tabularis* and *T. ciliata* were negatively influenced by early growing season temperatures (Mar-Apr), whereas *L. speciosa* growth was inversely related to average annual gridded T_{mean} (Fig. 7). We did not find any significant spatial correlations between tree-growth and precipitation. On a regional scale, tree radial growth was not directly correlated with SSTs of the Pacific, Indian, and Atlantic Oceans. Similarly, ISMI was not correlated with tree-growth in any species. However, SST anomalies of the Niño 3.4 region showed a significant negative effect on radial growth of the following year. The inverse synchronization of ENSO events and following year tree-growth was highest in *C. tabularis*, followed by *T. ciliata* and *L. speciosa* (Figs. 8, S5). The inter-connections between tree radial growth, local instrumental climate data sets and SST anomalies of the Niño 3.4 region are shown in the path diagram (Fig. 9).

3.3. Growth models

Multiple linear regression models were developed for all three species with the response variables identified in climate-growth analysis of each species. Model parameters and coefficients with their significance are provided in Table S3. *C. tabularis* explained highest variation ($r = 0.64$) followed by *T. ciliata* ($r = 0.60$) and *L. speciosa*

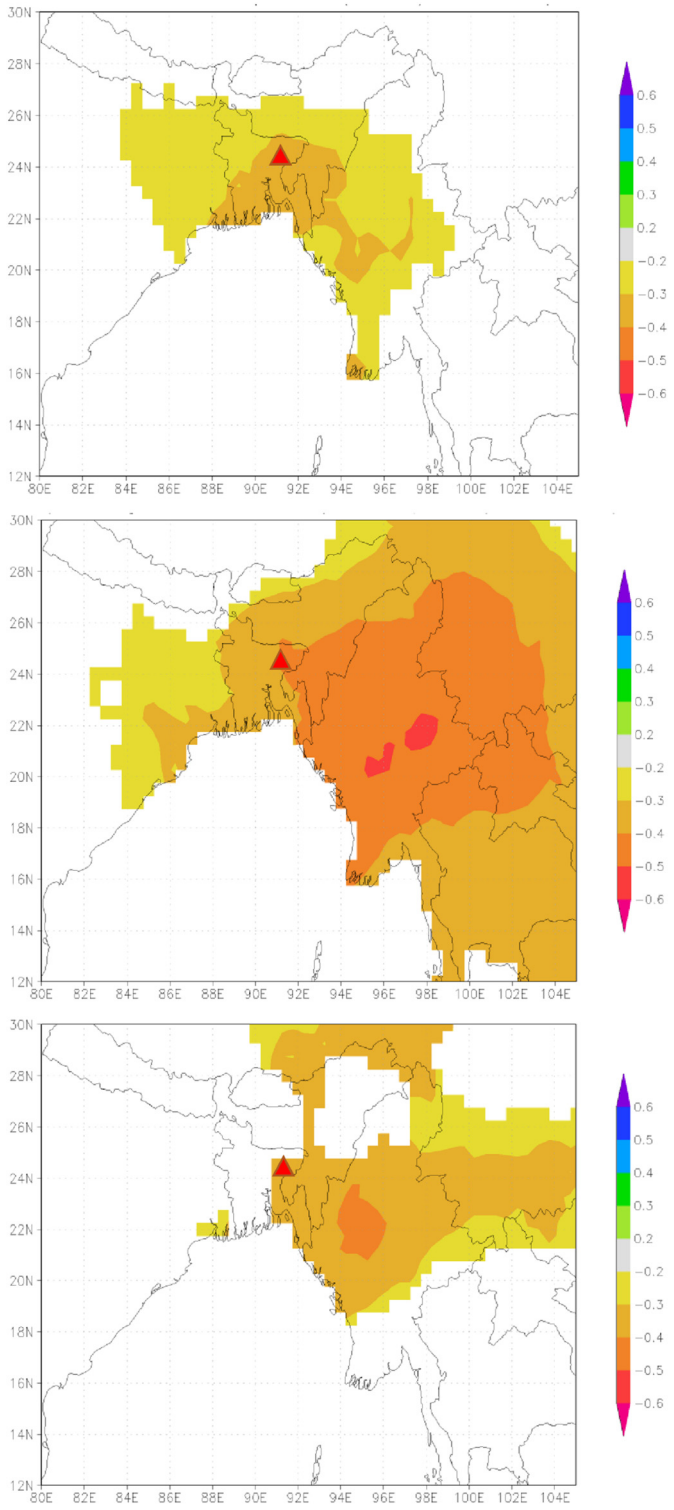

Fig. 7. Spatial correlations between RWI and global temperature data sets. Upper panel: Correlation between RWI of *C. tabularis* and current year March mean temperature; Middle panel: Correlation between RWI of *T. ciliata* and current year Feb-April mean temperature; Lower panel: Correlation between RWI of L. *speciosa* and annual mean temperature. Gridded temperature data represent the data set of CRU TS4.01 with 0.5 × 0.5° resolution over the period 1950–2015; Solid triangles indicate the study area, Color code represents Pearson correlation coefficients ($p < 0.05$).

($r = 0.51$). However, all three models passed the rigorous verification and cross-validation statistical tests (Table 3). The high correlations between observed and predicted ring-width indices (Fig. 10), good predictive skills as indicated by a relative high RE, CE, low MSE, non-significant values in DW test (Residuals from the regression are random and lack of autocorrelation in time series), and no temporal trend in the residuals (Fig. 10) suggest that the models can be considered sufficiently robust to be used for predicting growth outside the calibrated time period (Fritts, 1976).

3.4. Predicting tree growth until the end of the current century

The validated models were used to simulate growth for the 1950–2015 observed climate period and then predicted growth for the period over 2016–2100 under three climate change scenarios (RCP 4.5, RCP 6.0, and RCP 8.5). RWI will decline over time under all climate change scenarios in all three species (Fig. 11). Likewise, the number of years with above average growth will decrease at the end of the current century, with a sharp decrease during the 2060s (Fig. 11). Overall, tree-growth was predicted to decline by 20% in all species under the RCP 8.5 scenario, followed by 11.3% and 9% under RCP 6.0 and RCP 4.5, respectively. We did not find any significant differences in predicted growth changes among the species.

4. Discussion

4.1. Crossdating quality and reliability of tree-ring chronologies

Individual tree-ring series of each species were successfully crossdated within and between trees of the same species. A high series intercorrelation in all species (0.45–0.54) and a high mean GLK value (0.65–0.73) provided strong evidence of successful crossdating of ring-width series and indicated that the measured growth rings were indeed annual (Stahle et al., 1999). The annual nature of growth-ring formation in *C. tabularis* was also confirmed in a previous study (Rahman et al., 2017). *T. ciliata* also forms annual growth rings (Baker et al., 2005; Heinrich and Banks, 2006; Vlam et al., 2014; Shah and Mehrotra, 2017). Likewise, growth-ring formation in L. *speciosa* was described as annual in a preliminary study (Bhattacharyya and Yadav, 1989). Derived tree-ring chronologies of all three species contained strong environmental signals since the mean EPS was high (0.90–0.91) with *C. tabularis* having the highest mean EPS value (0.91). The SIC, MS, SNR and other statistical parameters values suggest that the chronologies are statistically robust, contain adequate signals and are suitable for standard dendroclimatic analysis.

The chronology signals we reported in this article are of similar magnitude reported in other studies on tropical trees (Brienen and Zuidema, 2005; Bräuning et al., 2009; Battipaglia et al., 2015; Chen et al., 2015; Pucha-Cofrep et al., 2015; Locosselli et al., 2016; Rahman et al., 2017). However, the running EPS dropped below the commonly used threshold value (EPS = 0.85) in all three species before the 1920s, although this threshold value is not a strict measure of the reliability of a chronology (Buras, 2017). Nevertheless, the reliable part of our shortest chronology (*T. ciliata*) spanned over 70 years which exceeded the available local instrumental climate data sets for our study sites (1950–2015, 66 years). The strong positive correlations among the chronologies ($p < 0.01$) and the synchronization of growth suppression in marker years in all three species generally imply that some common environmental factors triggered the inter-annual growth variability of these species in our study region.

4.2. Influence of local and global climate on tree growth

We found significant negative correlations between tree radial growth and temperatures (T_{mean}, T_{min}, and T_{max}). Radial growth in *C. tabularis* and *T. ciliata* were negatively affected by all T_{mean}, T_{min}, and

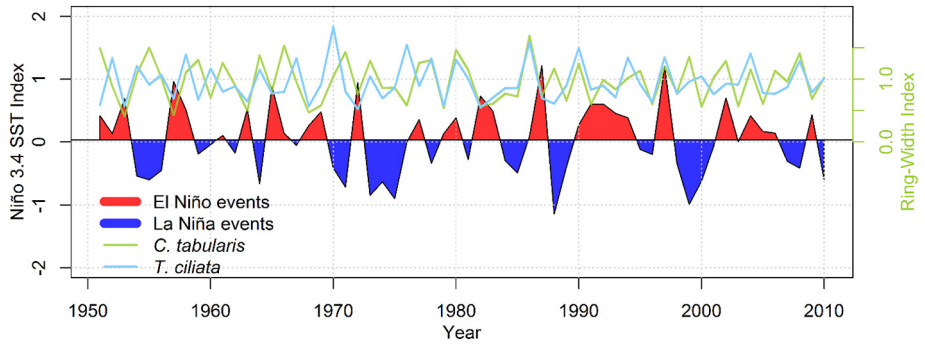

Fig. 8. Influence of Niño 3.4 SST anomalies (JJAS) on tree radial growth of the following year. For clarity, current year Niño 3.4 SSTs and following year tree growth are presented contemporaneously by shifting the time scale of the ring-width series by one year.

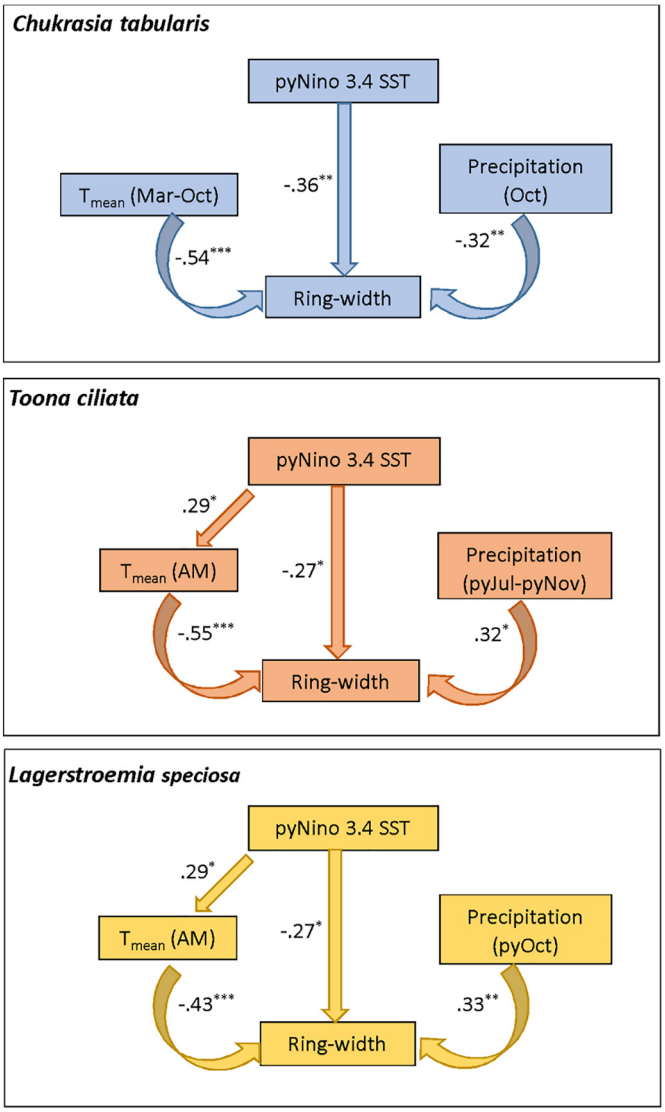

Fig. 9. Path diagram showing the influence of climatic variables on the growth of three Bangladeshi moist forest tree species. AM = Annual mean, py = previous year; Values are correlation coefficients significant at *p < 0.05, **p < 0.01, ***p < 0.001 level (2-tailed).

T_{max} whereas *L. speciosa* growth was influenced by T_{mean} and T_{min}. Pre-monsoon temperatures had a dominating role to influence growth in all species (Fig. 6). In line with the local temperature signal, our tree-ring chronologies also contained a regional temperature signal as indicated by the strong spatial correlation (negative) between the chronologies and seasonal gridded temperature data sets (Fig. 7). The negative relationship between tree radial growth in the early and later growing season with concurrent temperatures is most likely linked to the higher evapotranspiration outside of the main summer monsoon season. An increase in temperature particularly during the hot and dry pre-monsoon season (early growing season) further increases water stress, resulting in tree growth decline. In line with the current study, temperature-driven higher evapotranspiration caused growth decline of the same species in some earlier studies (Rahman et al., 2017; Vlam et al., 2014). Inverse relationships between tree-growth and temperatures were found in many tropical forest sites (Fichtler et al., 2004; Buckley et al., 2007; Clark et al., 2003, 2010; Dong et al., 2012; Vlam et al., 2014; Locosselli et al., 2016; Rahman et al., 2017).

Heat-induced air water potential deficit and higher autotrophic respiration are likely to be linked with reduced carbon assimilation in higher plants (Clark, 2007; Feeley et al., 2007; Galbraith et al., 2010; Choat et al., 2012). It is noted that higher temperatures potentially increase respiration rates in tropical forests (Meir et al., 2008). Moreover, higher temperatures increase the maintenance costs of plant tissues (Lloyd and Farquhar, 1996). Controversially, it is argued that plants can quickly acclimate to such changes in temperatures (Atkin et al., 2005; Lloyd and Farquhar, 2008). However, this acclimation process is generally applied for data sets covering a short period of time (Saxe et al., 2001; Shaver et al., 2000), such as data derived from short-term permanent sample plot, and hence may not apply to our results.

A significant negative correlation was found between current year October precipitation and tree-growth of *C. tabularis*. At the end of monsoon season, the soils become moisture saturated. An increase in precipitation in October may further increase soil moisture in our study sites. Since *C. tabularis* prefers well drained soils and cannot withstand wet and heavy soils (Orwa et al., 2009), it is possible that high soil moisture content in October negatively affected growth of *C. tabularis* in our study site. Our results, however, contrast with earlier studies in tropical dry forests or savannas, reporting positive correlations between tree-growth and precipitation (Enquist and Leffler, 2001; Fichtler et al., 2004; Brienen and Zuidema, 2005; Schöngart et al., 2006; Trouet et al., 2006; Shah et al., 2007; Gebrekirstos et al., 2008; Ram et al., 2008; Pucha-Cofrep et al., 2015; Locosselli et al., 2016). The differences in soil moisture availability and total annual precipitation of our study sites might have caused this variation in growth response to climate in other tropical forest sites. Since our study area receives approximately 2300 mm of rainfall annually and contains sufficient moisture content in the soils, our results are not directly comparable to dry tropical forest sites.

We observed a positive correlation of *T. ciliata* growth with previous year July precipitation and *L. speciosa* growth with previous year October precipitation. We found significant autocorrelation in both *T. ciliata* and *L. speciosa* (Table 2) which likely explains the positive correlation between previous year precipitation and current year tree

Table 3
Calibration and verification statistics of multivariate models for predicting tree ring-width indices from climatic variables. For description of statistical tests and the required values for successful model verification are stated in the methodology section.

		Calibration (1950–1990)	Validation (1991–2015)	Calibration (1991–2015)	Validation (1950–1990)	Final model (1950–2015)	Remarks on verification test
C. tabularis	R^2	0.44	0.35	0.35	0.44	0.41	
	r	0.66	0.60	0.60	0.66	0.64	
	p	0.000	0.009	0.009	0.000	0.000	
	RE		0.34		0.43		Passed
	CE		0.33		0.41		Passed
	MSE	0.07	0.04	0.04	0.07	0.06	Passed
	PMT	2.75	2.85	2.85	2.75	3.91	Passed
	DW	2.41	2.8	2.8	2.41	2.54	Passed
T. ciliata	R^2	0.42	0.31	0.31	0.42	0.36	
	r	0.65	0.56	0.56	0.65	0.60	
	p	0.000	0.018	0.018	0.000	0.000	
	RE		0.24		0.41		Passed
	CE		0.23		0.40		Passed
	MSE	0.06	0.04	0.04	0.06	0.05	Passed
	PMT	2.87	2.29	2.29	2.87	2.6	Passed
	DW	2.6	2.17	2.17	2.6	2.51	Passed
L. speciosa	R^2	0.19	0.40	0.40	0.19	0.27	
	r	0.48	0.63	0.63	0.48	0.51	
	p	0.03	0.004	0.004	0.03	0.000	
	RE		0.37		0.29		Passed
	CE		0.36		0.28		Passed
	MSE	0.05	0.02	0.02	0.05	0.04	Passed
	PMT	1.62	2.37	2.37	1.62	2.26	Passed
	DW	2.56	3.14	3.14	2.56	2.65	Passed

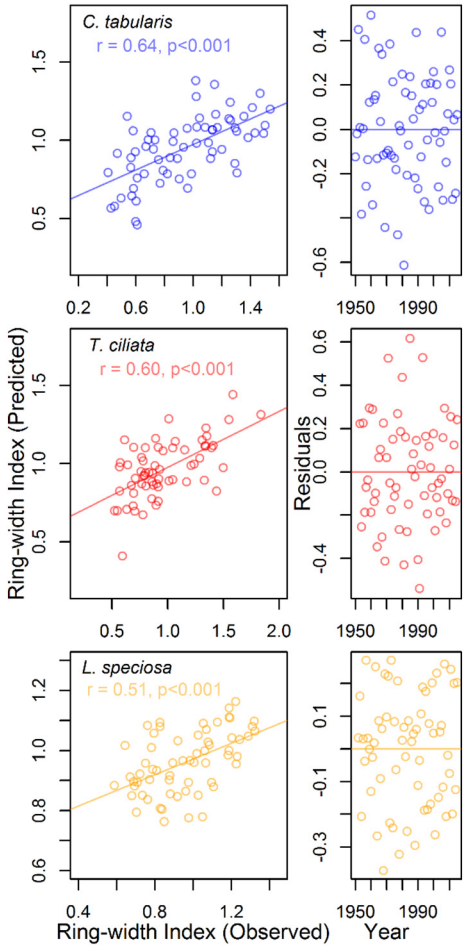

Fig. 10. Observed and predicted RWI and the residual values of predicted models of three Bangladeshi moist forest tree species.

growth in these species. The first-order autocorrelation of a tree-ring chronology is an indicator that ring width of the previous year may have an impact on ring width in the current year (Fritts, 1976), probably by strong carry-over effects of carbon assimilated during the previous vegetation period and stored in wood parenchyma cells (Bréda et al., 2006; Steppe et al., 2015). Higher precipitation in the monsoon and post-monsoon seasons of previous year may be useful for tree growth in the early growing season which starts around February.

Niño 3.4 region SST anomalies inversely affected tree-growth in the following year of El Niño events, implying that El Niño events have a delayed influence on tree-growth. The influence of ENSO events on tree growth is clearly reflected in the growth variability spectrum of each species with a 2–4 years periodicity (Fig. 5). The climate of Bangladesh is modulated by SSTs of the Equatorial Pacific and the Indian Ocean (Cash et al., 2010). The modulation of local climate by the regional climate drivers and subsequent influences on tree radial growth was found in the earlier study on *C. tabularis* (Rahman et al., 2017) in Bangladesh, reporting that SSTs of Niño 3.4 region increase temperatures in the following year's growing season leading to tree growth decline. It is therefore possible that tree-growth in all the studied species declined in the year following an El Niño event. However, *C. tabularis* was affected more than *T. ciliata* and *L. speciosa* by Niño 3.4 SST anomalies (Fig. 9). Differences in ecological guild likely explain such differences in growth response to El Niño events.

4.3. Tree growth response to future climate change

We developed statistically verified and cross-validated models for three species and projected that tree radial growth will decline at the end of the current century by 9–20% depending on the RCP scenarios used. The mean temperatures recorded in the local meteorological station close to our study sites showed a significant increasing trend (Fig. 2) and have risen by 1.19 °C in the last 66 years. According to a multimodel mean of CMIP5, temperature will increase by 2.0 ± 0.4 °C under RCP 6.0 and 3.3 ± 0.6 °C under RCP 8.5 (Collins et al., 2013). At the same time, precipitation has been predicted to increase in future (IPCC, 2013), although we did not find any significant trend in the last 66 years in our study area (Fig. 2).

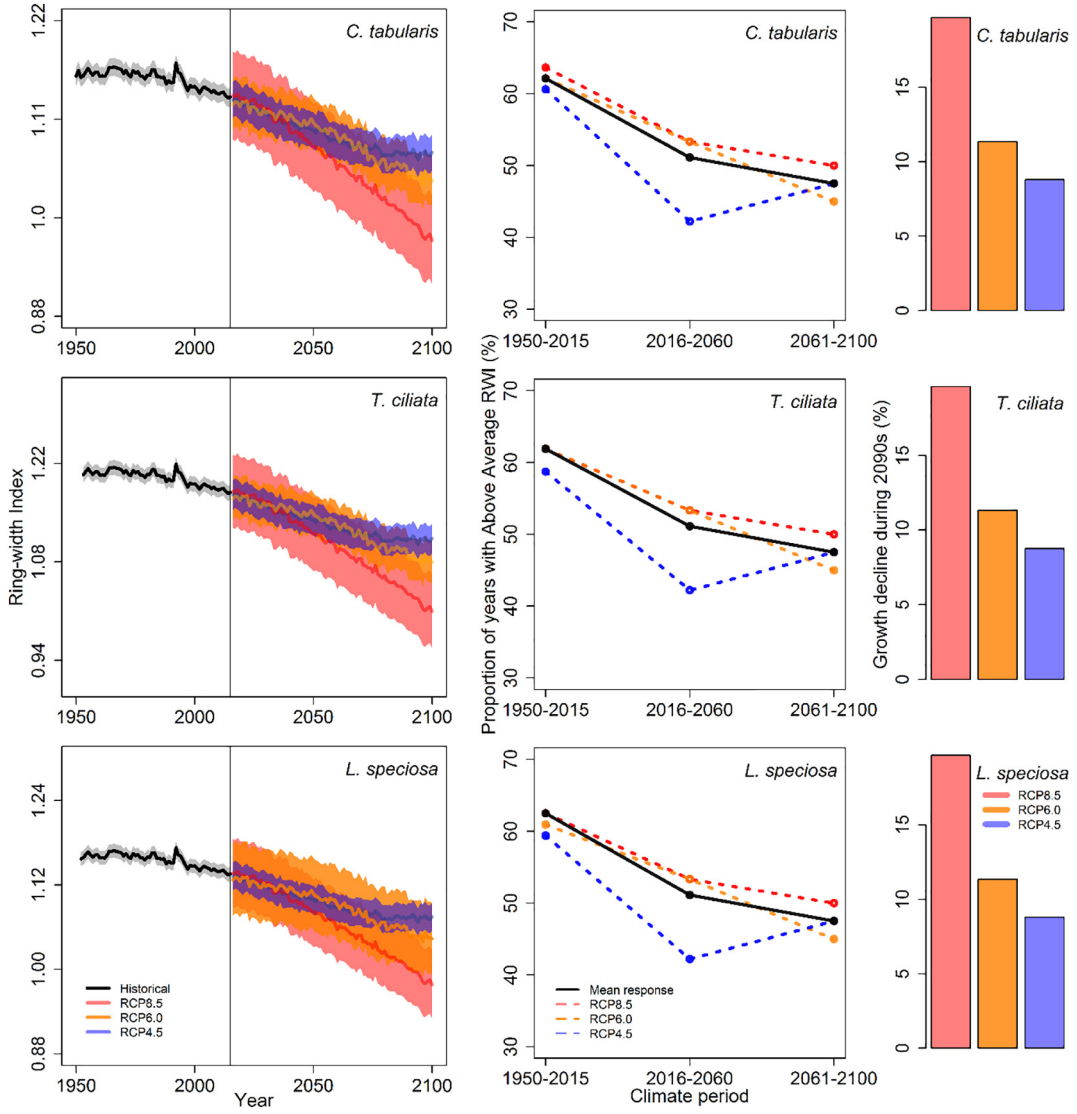

Fig. 11. Projected changes in tree radial growth under different climate change scenarios. For the description of RCP scenarios the authors are referred to the method section. Shaded areas in the left panels indicate standard deviations.

The stronger negative correlation of tree radial growth with temperatures as compared to the weaker correlations with precipitation and the relative importance of these climatic variables in the developed model clearly indicate the dominating role of global warming on the predicted growth decline of our species. Due to the lack of similar studies in moist tropical forests, we are unable to directly compare our results of predicted growth changes with related studies. However, a similar magnitude of growth reductions were predicted during 2080–2100 for a Mexican dry forest tree under climate change (Brienen et al., 2010). Species-specific growth decline under climate change was also reported in warm temperate climatic condition in Melbourne, southeastern Australia (Nitschke et al., 2017). However, we did not find any significant difference in the magnitude of predicted growth reduction among the three studied species. Differences in climatic conditions and plant functional types do not permit direct comparison between two studies. Although our species are from two ecological guilds (pioneer and shade tolerant), similar growth responses to changing climate likely imply that climate influence dominated over the role of functional traits of species in changing climate.

It is important to note that we did not take possible CO_2 effects on tree growth into account in our models. It is claimed that elevated CO_2 can stimulate tree growth (Phillips et al., 2008; Lewis et al., 2009) by increasing water use efficiency (Wullschleger et al., 2002; Nock et al., 2011). Many other studies, however, reported that elevated CO_2 was not related to tree-growth. In a plot based study in a tropical rain forest in Costa Rica, Clark et al. (2010) showed that annual wood production was linked to climatic variation but not to increasing CO_2. Similarly, elevated CO_2 was reported to increase water use efficiency of tropical trees species but did not stimulate tree radial growth (Nock et al., 2011; Peñuelas et al., 2011; van der Sleen et al., 2014). Similar findings were reported from temperate (Lévesque et al., 2014), Mediterranean (Brito et al., 2016; Martínez-Sancho et al., 2018), and subtropical forests (Li et al., 2017), concluding that climate impact has overridden the potential CO_2 fertilization on tree radial growth in South Asian moist tropical forests.

In conclusion, declining tree growth in our studied species may have important implications for forest management, because these species have widely been planted for timber production across the tropics. If the observed growth decline in the studied species occurs in other tropical forest regions as well, it could affect the carbon balance of tropical forests in general. It is therefore important to extend such studies on long-term growth trends on the species level in a climate change context across the tropics.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gloplacha.2018.08.008.

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